Temporal Changes of Populations and Trophic Relationships of Wintering Diving Ducks in Chesapeake Bay

Matthew C. Perry, Alicia M. Wells-Berlin, David M. Kidwell and Peter C. Osenton

USGS Patuxent Wildlife Research Center, 12100 Beech Forest Road, Laurel, Maryland 20708 USA
Internet: mperry@usgs.gov

Abstract.—Population and trophic relationships among diving ducks in Chesapeake Bay are diverse and complex as they include five species of bay ducks (*Aythya* spp.), nine species of seaducks (Tribe Mergini), and the Ruddy Duck (*Oxyura jamaicensis*). Here we considered the relationships between population changes and diet over the past half century to assess the importance of prey changes to wintering waterfowl in the Bay. Food habits of 643 diving ducks collected from Chesapeake Bay during 1999-2006 were determined by analyses of their gullet (esophagus and proventriculus) and gizzard contents and compared to historical data (1885-1979) of 1,541 diving ducks. Aerial waterfowl surveys, in general, suggest that six species of seaducks were more commonly located in the meso- to polyhaline areas of the Bay, whereas five species of bay ducks and Ruddy Ducks were in the oligo- to mesohaline areas. Seaducks fed on a molluscan diet of Hooked Mussel (*Ischadium recurvum*), Amethyst Gemclam (*Gemma gemma*), and Dwarf Surfclam (*Mulinia lateralis*). Bay ducks and Ruddy Ducks fed more on Baltic Macoma (*Macoma balthica*), the adventive Atlantic Rangia (*Rangia cuneata*), and submerged aquatic vegetation (SAV). Mergansers were found over the widest salinity range in the Bay, probably because of their piscivorous diet. Each diving duck species appears to fill a unique foraging niche, although there is much overlap of selected prey. When current food habits are compared to historic data, only the Canvasback (*Aythya valisineria*) has had major diet changes, although SAV now accounts for less food volume for all diving duck species, except the Redhead (*Aythya americana*). Understanding the trophic-habitat relationships of diving ducks in coastal wintering areas will give managers a better understanding of the ecological effects of future environmental changes. Intensive restoration efforts on SAV and oyster beds should greatly benefit diving duck populations.

Key words.—Diving ducks, seaducks, bay ducks, SAV, food habits, trophic relationships, Chesapeake Bay.

Waterbirds 30 (Special Publication 1): 4-16, 2007

Biologists and managers of migratory waterfowl (Anatidae) are aware of the historic value of Chesapeake Bay as a wintering ground of North American swans, geese, and ducks. The rich estuarine habitats of Chesapeake Bay provide abundant food resources at a mid- continent latitude favorable to wintering waterfowl. Chesapeake Bay received early attention from explorers, naturalists, artists, and hunters who were attracted to this huge estuary and marveled at the magnitude of wintering waterfowl populations that existed there (Audubon 1840; Arber 1910). Populations seemed inexhaustible and a "myth of superabundance" prevailed among Americans (Udall 1963). By the early 1900s, however, unregulated market hunting had placed populations of ducks, geese, and swans in sharp decline in Chesapeake Bay and other North American wintering areas (Forbush 1912; Matthiessen 1959; Elman 1980). Although not native to the Chesapeake Bay, the extinction of the Labrador Duck (*Camptorhynchus labradorius*), served as a warning that a further loss of species may occur if greater protection of waterfowl was not forthcoming (Grinnell 1901; Forbush 1913; Salyer 1934).

Numerous efforts to reverse the downward trend in waterfowl abundance were initiated around the turn of the century, culminating in the passage of the Migratory Bird Treaty Act of 1918 (Reed and Drabelle 1984). This act put all migratory birds under the control of the Federal government and protected all species. Hunting regulations were established by the Federal government with guidelines to the states for species whose populations could withstand harvest.

Historically, most of the huge flocks of "puddle" (or dabbling) ducks (Anatinae) occurred in oligohaline (freshwater) areas of the Bay, where they fed on lush stands of submerged aquatic vegetation (SAV), especially during early winter (Stewart 1962). Diving ducks (Aythyinae and Oxyurinae), in general, had a broader distribution in the Bay with greatest numbers in the mesohaline (brackish water) areas of the main stem and adjoining estuarine tributaries (Cottam 1939). The Canvasback (*Aythya valisineria*) was the most prized game duck, pursued by market and sport hunters alike (Walsh 1971). In this paper, diving ducks include five species of bay ducks (or Pochards, *Aythya* spp.), nine species of seaducks (Tribe Mergini), and the Ruddy Duck (*Oxyura jamaicensis*).

Although populations of diving ducks rebounded from low numbers in the early 1900s (Perry *et al.* 1981), declines in the 1960s raised new concerns about the status of Canvasbacks and other species (Haramis 1991a,b). Restrictive hunting regulations were imposed on Canvasbacks during the 1970s and early 1980s, but other species of ducks and geese were harvested during the 1960-80s, and the Bay maintained the reputation as one of the most productive estuaries in the world for winter concentrations of waterfowl.

Changes in the distribution and abundance of diving ducks in Chesapeake Bay may reflect changes in the quality of Bay habitat or broader continental or regional changes in populations. Major declines in most species of Bay diving ducks since 1955, parallel population changes in the Atlantic Flyway and the United States (Perry *et al.* 1981). Although wintering habitat is essential, breeding habitat in northern areas is also necessary to maintain abundant Bay waterfowl populations. Most habitat loss and degradation are related to increasing human populations in North America, which have destroyed or degraded approximately 40% of the original wetland habitats available to waterfowl (Perry and Deller 1996).

Among the diving ducks, the seaducks recently have received increased management attention from a continental perspective as many North American populations (13 of the 15 species) have declined (Kehoe 1994; Goudie *et al.* 1996; Petersen and Hogan 1996; Elliot 1997). Surveys of seaducks wintering on the Atlantic coast (1991-99) have suggested major declines for the Long-tailed Duck (*Clangula hyemalis*), Black Scoter (*Melanitta nigra*), and Surf Scoter (*Melanitta perspicillata*), whereas the White-winged Scoter (*Melanitta fusca*) increased in numbers (Caithamer *et al.* 2000). Waterfowl managers recognize, however, that estimates of seaducks are the most unreliable, as some large flocks are not seen due to the great distance the ducks sometimes frequent from shore. In general, surveys of wintering duck populations are criticized for the variability of results caused by changing observers, habitats, and equipment (Heusmann 1999). Surveys sponsored by the U.S. Fish & Wildlife Service (USFWS) are continuing to help delineate the size and location of Atlantic coast seaduck populations (D. Forsell and M. Koneff, USFWS, pers. comm.) and new studies are underway to determine causes for the declines of seaduck populations.

Loss of submerged aquatic vegetation and changes in the quantity and quality of available invertebrate foods due to degradation of water quality within Chesapeake Bay has been a major contributing factor to some population declines (Orth and Moore 1983; Perry and Deller 1996). Many other factors related to human population increases have been implicated in the degradation of Chesapeake Bay (Horton and Eichbaum 1991), and are thought to negatively affect duck populations. The objectives of this paper are to show long-term trends of diving duck populations and to relate these changes to possible changes in the habitats used in the winter by diving ducks and the foods they obtain in these habitats.

METHODS

Abundance and Distribution

Numbers and locations of wintering diving ducks in Chesapeake Bay were determined using data from aerial Mid Winter Waterfowl Surveys (MWS) conducted from single-engine aircraft by USFWS in cooperation with state wildlife agencies (Serie and Raftovich 2006). Surveys have been flown since 1948 over near-shore tidal areas of the Bay at the altitude of approximately 50 m. Surveys in early years were incomplete (Perry 1987) so data used in this report are from the period 1955-2006. Surveys were conducted during mid-winter (early January) and all ducks observed were identified by species and their numbers estimated. Because of the difficulty in identifying the two scaup (*Aythya* spp.) and three scoter species (*Melanitta* spp.) from the air, these species were grouped together as scaup and scoter species, respectively.

These surveys can help to identify long-term trends in waterfowl numbers and to make comparisons with Flyway and continental estimates. However, because of the number of variables inherent in the surveys (Eggeman and Johnston 1989; Heusmann 1999) and the lack of replication and determination of species detection rates (Nichols *et al.* 2000), interpreting annual population changes should be done with extreme caution. Because statistical assumptions are often violated, regression analyses were not conducted, but annual estimates are shown in results.

Food Habits

Current food habits were determined by analyses of the digestive tracts of 643 ducks obtained from hunters or from law-enforcement personnel during the winters of 1999 to 2006. All ducks were shot during daylight hours, mostly at dawn or dusk, and were frozen until examination. Ducks were weighed, aged, and sexed before dissection and age and sex were confirmed during dissection. The gullet (esophagus and proventriculus) and gizzard were removed and maintained separately for analyses. Both organs were used in interpreting food choices from a diversity perspective. Gullet samples containing food were low, so data from both gizzard and gullets were analyzed in interpreting food choices quantitatively. The problem of bias associated with gizzard samples, i.e., differential digestion of hard- versus soft-bodied items (Swanson and Bartonek 1970), is mitigated in Chesapeake Bay by a predominance of hard-bodied organisms in the diet, mainly shellfish (Perry and Uhler 1988). A recent comparison of gullet and gizzard contents of diving ducks in Chesapeake Bay confirmed this notion and validates the use of gizzard contents for interpreting diving duck food habits in the Bay (DMK and MCP, unpublished data).

Both gullet and gizzard from ducks were frozen until analyses were conducted. In the laboratory, contents were removed and separated by species, and dry weights and volumes were determined for each sample. Frequencies of occurrence and average percent volume (aggregate percent) of the food items were determined for each duck species (Martin *et al.* 1946; Swanson *et al.* 1974; Perry and Uhler 1988).

Data from current food habits analyses were compared to data from three periods of historic food habits analyses for diving ducks on the Chesapeake Bay collected between 1885 and 1959 (Cottam 1939; Stewart 1962), between 1959 and 1968 (C. Rawls, University of Maryland, unpublished report), and between 1972 and 1979 (Munro and Perry 1981; Perry and Uhler 1988). All historic data were recalculated to exclude agricultural grains that were likely obtained from humans as bait at hunting blinds or from feeding stations along residential shorelines. Comparisons were made among total plant and animal food categories for the four different time periods using a standard analysis of variance and t-test statistics. Analysis of variance was also used to determine if there were significant differences in the lengths of Hooked Mussels (*Ischadium recurvum*) consumed among the three scoter species. All tests were considered significant at the 5% level.

RESULTS

Abundance and Distribution

Based on January aerial surveys, Chesapeake Bay has wintered on average approximately one million waterfowl annually, and approximately 70% of these birds are swans, geese, and puddle ducks. Diving ducks (bay ducks, seaducks, and Ruddy Ducks) make up the remaining 30% or 300,000 waterfowl in the Bay. Bay ducks represent the largest proportion of diving ducks and have averaged over 231,000 ducks per year during the 52-year survey period (Table 1). Ruddy Duck populations have averaged over 51,000 during the 52-year period (Table 1). Because bay ducks and Ruddy Ducks are generally highly visible and largely distributed in near-shore waters, their populations are considered to be accurately covered by the survey (Fig. 1).

Seaduck populations combined have averaged over 47,000 annually (Table 1) and overall have been stable, but have been highly variable among years (Fig. 2). However, because most seaducks are located far from shore in areas that are not covered by the Mid Winter Waterfowl Survey, the survey is considered inadequate to estimate total numbers of seaducks wintering on the Chesapeake Bay. Special transect surveys have been designed to more adequately cover seaducks and other open-water species (D. J. Forsell, USFWS, unpublished data).

The distribution of diving ducks between Maryland and Virginia is proportional to the amount of open water area of the Bay, which is approximately 67% for Maryland and 33% for Virginia. On average for the 52-year survey period, 61% of the bay ducks were located in the Maryland portion of the Bay and 39% in Virginia (Table 1). Ruddy ducks also were proportionally distributed in the two states with 60% in Maryland and 40% in Virginia. Seaducks tended to occur on average in greater numbers in Maryland (76%) compared to Virginia (24%). The Long-tailed Duck (*Clangula hyemalis*) and Common Goldeneye (*Bucephala clangula*) were both more common in Maryland with 87% of their populations being recorded there.

In an earlier analysis, diving ducks wintering in Chesapeake Bay during the 1950-95 period accounted for 23% of Atlantic Flyway and 9% of North American populations (Perry and Deller 1995). There was a decline in all five pochard species, as well as Common Goldeneye, and Ruddy Ducks during

Table 1. Mean number and percentage of diving ducks by state in Chesapeake Bay from the aerial Mid Winter Waterfowl Survey, 1955-2006.

	Maryland	Virginia	Chesapeake Bay
Bay Ducks (Aythyini)			
Canvasback	65,142 (63%)	39,067 (37%)	104,209
Redhead	17,279 (64%)	9,592 (36%)	26,870
Ring-necked Duck	4,791 (74%)	1,666 (26%)	6,457
Scaup (Greater and Lesser)	54,188 (58%)	39,740 (42%)	93,928
Total Bay Ducks	141,400 (61%)	90,064 (39%)	231,464
Stifftail (Oxyurini)			
Ruddy Duck	31,016 (60%)	20,358 (40%)	51,374
Seaducks (Mergini)			
Long-tailed Duck	3,865 (87%)	557 (13%)	4,421
Scoter (species combined)	6,818 (75%)	2,272 (25%)	9,089
Bufflehead	9,433 (66%)	4,816 (34%)	14,249
Common Goldeneye	11,034 (87%)	1,590 (13%)	12,624
Merganser (species combined)	5,438 (71%)	2,180 (29%)	7,618
Total Seaducks	36,146 (76%)	11,360 (24%)	47,506
Total Ducks	208,562 (63%)	121,782 (37%)	330,344

the period 1950-95. Scoter and Long-tailed Duck populations remained stable, whereas Bufflehead (*Bucephala albeola*) and merganser species were the only diving duck species that increased in numbers during the same period.

During the twelve-year period of 1995-2006, populations of some bay ducks and the Ruddy Duck increased substantially (Fig. 3). Populations of Ruddy Ducks increased by 300% and Ring-necked Ducks (*Aythya collaris*) numbers increased by almost 400%.

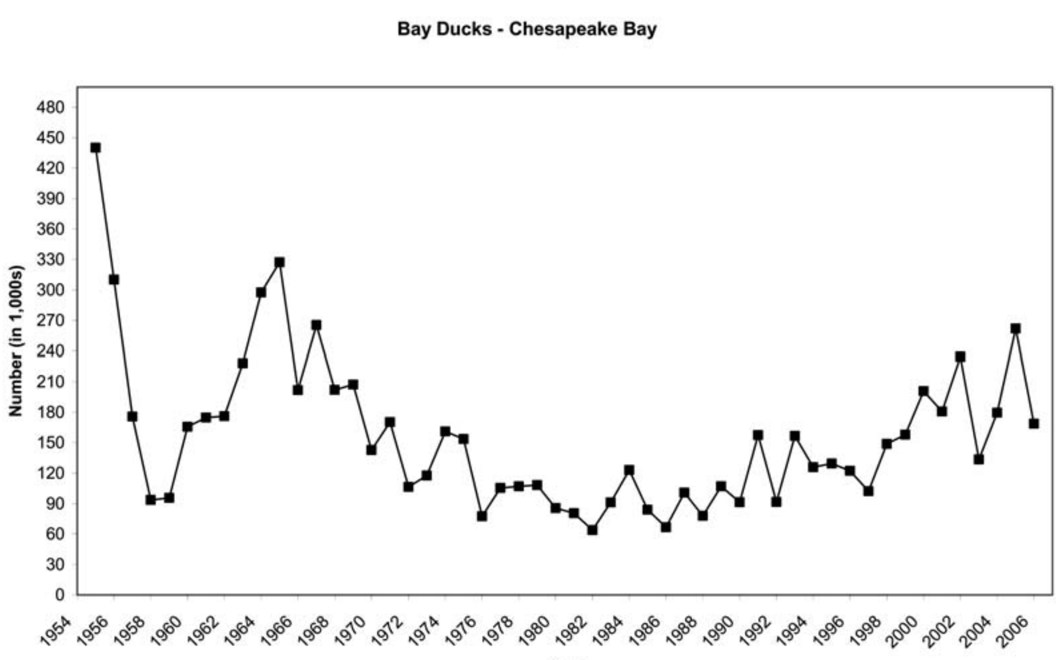

Figure 1. Mid-winter Survey estimates of bay duck species (pochards) and Ruddy Ducks combined during the period from 1955 to 2006 for all areas of Chesapeake Bay.

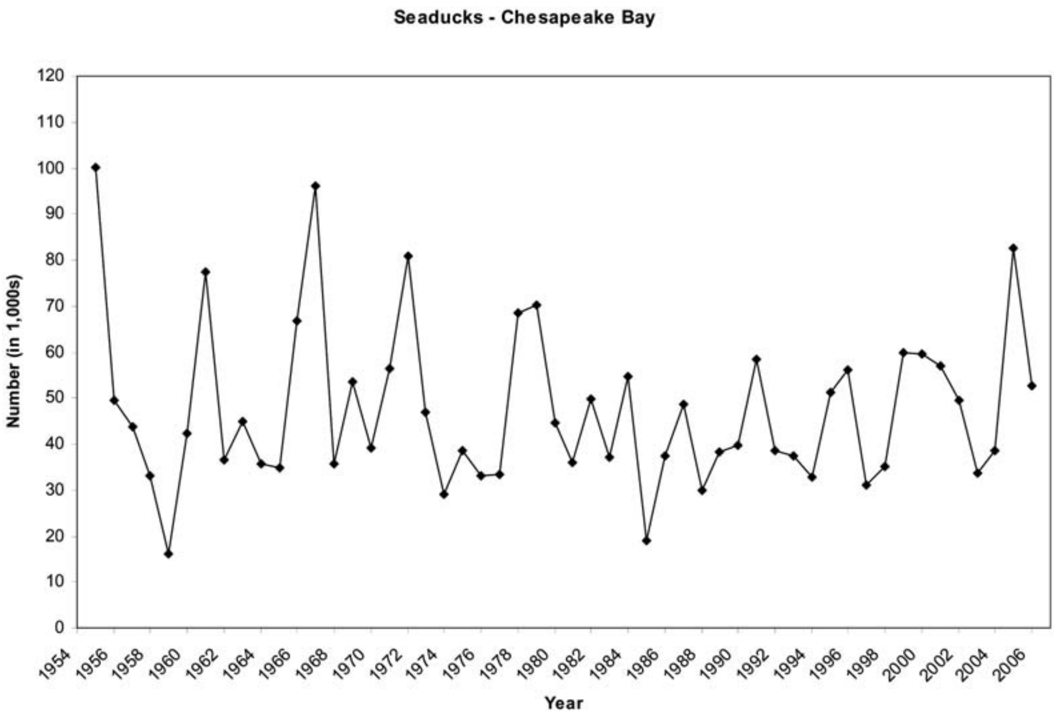

Figure 2. Mid-winter Survey estimates of seaduck species combined during the period from 1955 to 2006 for all areas of Chesapeake Bay.

Ring-necked Ducks, however, represent a small overall percentage of the bay ducks as they are more commonly found on freshwater lakes and ponds during winter and typically are not counted during aerial surveys. Redhead (*Aythya americana*) and Canvasback populations remained stable in recent years, but remain much lower than the earlier survey years (Fig. 3). Redhead populations reached an all time low count of 282 ducks on the Bay in 1992, although the long-term 52-year average was 26,870 (Table 1).

Recent surveys of seaducks in Chesapeake Bay during winter show increases in numbers of Buffleheads and Mergansers and declining numbers of Common Goldeneye and Long-tailed Ducks from earlier years (Fig. 4). Little change in scoter numbers was noted when compared to earlier surveys, but these estimates are considered to be low and should only be used with caution.

Food Habits

Some species of diving ducks have shown major long-term changes in foods eaten in Chesapeake Bay, whereas other species have shown no change. Current food habits show that vegetation now forms 19% of the food consumed by the twelve diving duck species compared to 42% in the three combined historic studies (Table 2). Current studies also show that there is a higher percentage (31%; N = 158) of vegetative food in the five species of pochards than is found in the food of the six species of seaducks (7%; N = 448) in the Bay (Table 2). Ruddy Ducks were intermediate of the bay ducks and seaducks in the amount of plant food they consumed (19%; N = 7).

Of the diving ducks, the Redhead is atypical in its nearly obligate SAV diet (N = 3). In the 1885-1959 and the 1972-79 historic data sets, vegetation constituted 99% (N = 86) and 97% (N = 7), respectively, of the diets. However, in the 1959-68 data, vegetation only formed 67% (N = 77) of the diet. Widgeongrass (*Ruppia maritima*) and American Eelgrass (*Zostera marina*) are the plants selected by Redheads in the current samples. Areas in the Bay where Redheads most fre-

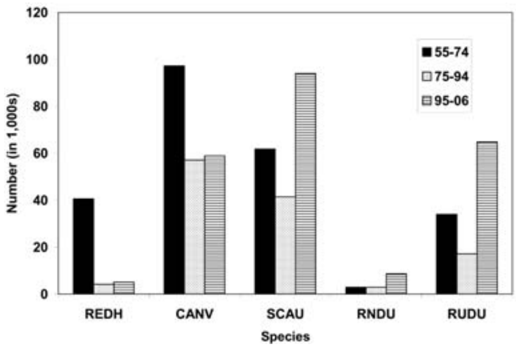

Figure 3. Population estimates of bay ducks (pochards) and Ruddy Ducks in Chesapeake Bay during time periods 1955-74, 1975-94, and 1995-2006 (REDH = Redhead; CANV = Canvasback; SCAU = Lesser and Greater Scaup; RNDU = Ring-necked Duck; RUDU = Ruddy Duck).

quently occur (e.g., Tangier Sound) are limited to localized stands of dense SAV species.

Stable populations of Canvasbacks suggest they have adapted to an invertebrate diet, mainly of Baltic Macoma (*Macoma balthica*; Perry and Uhler 1988), but at lower numbers compared to the 1970s (42%, N = 16 vs. 85%, N = 73). Recent analyses of Canvasback foods indicate an increase of vegetation consumed (32%, N = 16 vs. 24%, N = 519) from the 1960-70 period, but a decline in vegetation from the 1885-1959 period (32%, N = 16 vs. 71%, *n* = 47). The percentage of invertebrates in the diet of other pochards and Ruddy Ducks in the current data set increased as SAV declined in recent decades.

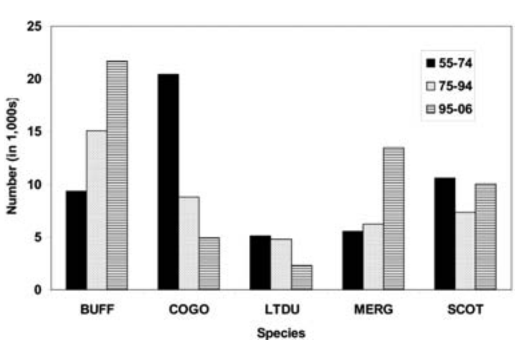

Figure 4. Population estimates of seaducks in Chesapeake Bay during time periods 1955-74, 1975-94, and 1995-2006 (BUFF = Bufflehead; COGO = Common Goldeneye; LTDU = Long-tailed Duck; MERG = Mergansers; SCOT = Scoters).

Canvasback and Lesser Scaup (*Aythya affinis*) were the only species of the twelve examined in the current analysis that had fed on Sweet Corn (*Zea mays*) and this food was only found in one individual of each species. The Canvasback, shot in Herring Bay, and the scaup, shot on the Chester River, represent only 0.3% of the total 643 diving ducks analyzed in the recent samples. These figures greatly differed from the diving ducks during the 1960s when an average of 12% corn or other grains (Wheat, *Triticum aestivum*; Barley, *Hordeum vulgaris*) was consumed. Redheads had the greatest amount (34.0%; N = 77) and no agricultural grains were found in the 27 Buffleheads or in the four Ruddy Ducks analyzed (C. Rawls, unpubl. data).

Both species of scaup fed on Hooked Mussels, but based on current data, Greater Scaup (*Aythya marila*) ate more (40%, N = 49 vs. 5%, N = 89) than Lesser Scaup (*Aythya affinis*). Lesser Scaup fed predominantly (57%) on the Atlantic Rangia (*Rangia cuneata*), but the Amethyst Gemclam (*Gemma gemma*) and other mollusks were also important components of its diet. Vegetation formed 28% of the diet of Greater Scaup with Sea Lettuce (*Ulva lactuca*) forming 21% of the total diet. Vegetation only made up 5% of the Lesser Scaup diet, but there was high diversity with 14 plant species identified.

Four percent of the lesser scaup diet was comprised of the introduced Asian Clam (*Corbicula fluminea*). This exotic species was first reported as food of Chesapeake Bay ducks in the James River area (Perry and Uhler 1981). This indicates that Lesser Scaup are feeding in freshwater areas, most likely the Potomac River, where this exotic clam thrives. Lesser Scaup was the only species of diving ducks that had fed on the Asian Clam in the current food habits analyses.

Both species of scaup fed on the Dark False Mussel (*Mytilopsis leucophaeta*), which was found in the gullet and gizzard of twelve scaup shot by hunters in the Chester River in January 2005. During the summer of 2004 a very unusual irruption of this clam occurred in low salinity areas of Bay tributaries. This irruption is believed to be caused by the unusu-

Table 2. Percent animal and plant foods for six species of seaducks, five species of bay ducks, and Ruddy Ducks from the Chesapeake Bay during four time periods: 1885-1959, 1959-1968, 1972-1979, and 1999-2006.[a]

	1885-1959			1959-1968			1972-1979			1999-2006		
	N	Animal	Plant	N	Animal	Plant	N	Animal	Plant	N	Animal	Plant
Bay Ducks												
Canvasback	47	29	71	246	60	40	273	91	9	16	68	32
Greater Scaup	36	60	40	9	66	34	40	67	33	49	72	28
Lesser Scaup	29	49	51	82	54	46	76	42	58	89	95	5
Redhead	86	1	99	77	33	67	7	3	97	3	0	100
Ring-necked Duck	98	19	81	10	7	93				1	100	Tr
Sub-Total	296			424			396			158		
Mean		32	68		44	56		51	49		69	31
Stifftails												
Ruddy Duck	63	72	28	4	65	35				37	81	19
Seaducks												
Black Scoter	24	90	10							44	88	12
Bufflehead	20	75	25	27	67	33	30	79	21	69	94	6
Common Goldeneye	14	47	53	45	77	23	21	75	25	4	82	18
Long-tailed Duck	90	88	12							38	99	1
Surf Scoter	68	88	12							283	98	2
White-winged Scoter	19	94	6							10	98	3
Sub-Total	235			72			51			448		
Mean		80	20		72	28		77	23		93	7
Total	594			500			447			643		
Mean		59	41		54	46		60	40		81	19

[a]Trace amounts (Tr) equal <0.5%. Time periods represent summaries of different data sets: 1885-1959—Munro and Perry 1983; 1959-68—Rawls Unpub Univ. of MD Report; 1972-79—Perry and Uhler 1988; 1999-2006—Perry Unpub. Data.

al dry period that changed salinity patterns within tributaries (V. Kennedy, Horn Point Lab, University of Maryland, pers. comm.).

Recent food habits analyses of Ruddy Ducks (N = 37) indicate that the Dwarf Surfclam (*Mulinia lateralis*) and two species of the Macoma Clam (*M. balthica* and *M. mitchelli*) made up 62% of their diet. Six species of plants formed 19% of their food, indicating a preference to feed in more fresh to brackish areas of the estuary. The amount of vegetation in the diet of Ruddy Ducks has declined slightly from historic levels (Table 2).

Food habits of the three species of scoters were similar, but there are subtle differences among species. All species fed predominantly on the Hooked Mussel, Amethyst Gemclam, and Dwarf Surfclam. However, Black Scoters (N = 44) selected Hooked Mussels (55%), Surf Scoters (*n* = 283) selected Dwarf Surfclam (35%), and White-winged Scoters (N = 10) selected the Amethyst Gemclam (39%) primarily. There were no differences ($F_{2,51}$ = 0.30, P > 0.05) in mean length of Hooked Mussels selected by Black Scoters (20.0 mm), Surf Scoters (18.7 mm), and White-winged Scoters (20.3 mm). Surf Scoters had consumed both the smallest (7.0 mm) and the largest (45.8 mm) Hooked Mussels eaten among the three scoter species.

Atlantic Rangia, Hooked Mussels, and unknown crabs (Decapoda) were the most important foods of a small sample of four Common Goldeneye collected in the Bay proper. Three other Common Goldeneye collected in March on the Susquehanna River had fed on Caddisfly (Tricoptera) larvae. Buffleheads fed predominantly on the Dwarf Surfclam (59%), which was much higher than any other seaduck or bay duck. Baltic Macoma and the Soft Shell Clam (*Mya arenaria*) were other major food items for Buffleheads (N = 69). The Bufflehead fed more on the mobile Yellow-jawed Clamworm (*Neanthes succinea*) than any other diving duck. The Long-tailed Duck (N = 38) selected the Dwarf Surfclam (30%) and the Gemclam (28%) as food in greatest amounts, but food habits of this species show a diverse diet of invertebrates (N = 24), especially mollusks and crustaceans.

More recently, the analyses of food of 283 Surf Scoters collected from different areas of the Bay showed local differences in food selection. Although benthic sampling was not conducted in each area, the major differences in food selected clearly showed that, as expected, ducks in the southern areas of the Bay were feeding on high mesohaline and polyhaline organisms, whereas ducks collected in the middle of the Bay were feeding on more mesohaline organisms. For example, in the southern Smith Island area Surf Scoters fed mainly on Stout Tagelus (*Tagelus plebieus*) and False Angelwing (*Petricola pholadiformis*) bivalves, whereas in the middle of the Bay Surf Scoters fed mainly on the Hooked Mussels and the Gemclams. Ducks fed on the Dwarf Surfclam in both areas indicating a broad tolerance of salinity tolerances and likely environmental adaptation for this species. Unfortunately, only a small sample of mergansers was available for food habits analyses. Two Hooded Mergansers (*Lophodytes cucullatus*) and one Red-breasted Merganser (*Mergus serrator*) had fed exclusively on fish (Osteichthyes), which were not identified.

DISCUSSION

Factors affecting diving duck populations in Chesapeake Bay include direct and indirect causes, including excessive shoreline development of Bay tributaries, increased year-round boat traffic, and increased levels of sediments and nutrients. Although food habits indicate changes in habitat for some species of diving ducks, especially the bay ducks since SAV has declined, other species of diving ducks show little changes in food habits and still are feeding on mollusk species that have traditionally formed the bulk of their diets in Chesapeake Bay (Stewart 1962) and in other wintering areas of the Atlantic Flyway (Stott and Olsen 1973). Species, like the bay ducks, which historically fed on SAV in shallow water, are more likely to be adversely affected by environmental changes in the Bay than molluscivorous species in slightly deeper water. Increases in nutrient inputs and sedimentation in these shallow water areas has been a causative factor in SAV decline and loss of habitat (Perry and Deller 1996). However, while seasonal hypoxia has typically occurred below the feeding depth of most diving ducks, recent expansion of the hypoxia area may be adversely affecting prey availability, especially immobile sessile prey. Availability of food is especially important in the fall and early winter when diving ducks are arriving to the Bay. Haramis *et al.* (1986) found that overwinter and annual survival probabilities were greater in Canvasbacks that had higher early winter body mass.

Mid Winter Surveys can be used to identify local shifts in populations, possibly caused by habitat changes. In an early review of diving duck populations in Chesapeake Bay, Perry *et al.* (1981) suggested that Canvasback and Redhead population changes in Chesapeake Bay during the 1970s did not reflect increases identified throughout the United States. They attributed this phenomenon to a more rapid degradation of the Bay wintering habitat and a shift in population to Virginia and North Carolina. Lovvorn (1989) suggested this was possibly due to higher density of clams in North Carolina and lower thermoregulation costs to the ducks. The present analysis does not seem to fully support the above hypotheses as Canvasback populations in recent years have been stable in Chesapeake Bay and have declined in North Carolina. Redhead populations, however, still are being affected by the loss of submerged aquatic vegetation in the Bay. These areas, however, are still greatly reduced from levels in the 1950s, contributing to much lower Redhead populations in the Bay. Redheads now are more commonly found in areas of North Carolina and the Gulf Coast (Florida and Texas), where there are more abundant stands of SAV for them as a food source (Haramis 1991b). Large restoration projects for SAV have been conducted for several decades and some feel offer promise, although overall there is concern for the future of SAV (Orth *et al.* 2006). Scaup population increases in the Bay during recent years are surprising based on continental declines of these two species (Austin *et al.* 2000). This result suggests that the Bay is attractive to wintering scaup and is providing an adequate food base for either or both species.

Although seaduck populations in Chesapeake Bay overall seem to be stable, there are signs that some species are in decline. The decline of the Common Goldeneye during the 52-year survey period is surprising when compared to Bufflehead increases (Fig. 4). These species have similar breeding and wintering requirements and select similar foods in winter. It would, therefore, be expected that they would respond similarly to environmental stressors and share similar mortality factors. It remains unknown why numbers of Common Goldeneye are declining on the Chesapeake Bay. Black Scoters have also declined and now represent the seaduck species of most concern in Chesapeake Bay and the Atlantic Flyway (Caithamer *et al.* 2000). Both Long-tailed Ducks and scoter populations were considered to be fairly low throughout North America when surveys began in 1950.

Major concentrations of Surf Scoters (10,000-20,000) have been observed near Holland Point and Poplar Island in mid Chesapeake Bay, whereas White-winged Scoters occur in greatest numbers (5,000-10,000) near the mouth of the Choptank River. Black Scoters are not found in large flocks in the Bay and appear to have a wider coast-wide distribution than the other two scoter species. The widespread distribution of Long-tailed Ducks in the Bay reflects their diverse diet.

Historic analyses indicate that fish are primary prey for all mergansers, although Hooded Mergansers also feed on invertebrates. The Hooded Merganser and Common Merganser (*Mergus merganser*) typically are found more in freshwater rivers, ponds, and reservoirs near the Bay tributaries, not in the main stem of the Bay (Stewart 1962). The 1960s analyses by Rawls (unpublished data) showed that four Red-breasted Mergansers had fed exclusively on unidentified fish, which he suggested were *Fundulus* sp. Stewart (1962) also reported *Fundulus* sp. as a food of Red-breasted Mergansers in the Bay, along with amphipod crustaceans (Amphipoda).

Food habits studies often stimulate the question of whether species are expressing dietary preferences or simply are consuming foods available in the environment. The food availability of diving ducks in Chesapeake Bay has been analyzed in past studies (Stewart 1962; Perry and Uhler 1988). Benthic sampling of the individual rivers and bays where Canvasbacks were collected in the 1970s revealed a close relationship between diet and the prey availability (Perry and Uhler 1988), which was mainly the Baltic Macoma clam. Bay-wide surveys done by Jorde and Haramis (Jorde *et al.* 1992) showed high numbers of this widely distributed clam in the Bay.

In general, infaunal clams seemed to be found in lower amounts in Black Scoters indicating they may be feeding more on epifauna than the other two scoter species. Some of the changes in the food habits of scoters could be directly related to the decline of Hooked Mussel availability, associated with the loss of the Eastern Oyster (*Crassostrea virginica*) bars. The major decline in the oyster population in the Bay, which is estimated to be 1% of the historic abundance (Newell 1988), could contribute to the low population of scoters. Oyster bars harbor a diversity of other invertebrates, such as small crabs and amphipods, on which scoters are likely to feed, adding to the importance of the oyster bars for diving ducks. The fact that scoters are feeding on the same size Hooked Mussel may result in the smaller Black Scoter being at a disadvantage to the larger White-winged and Surf Scoters when competing for limited mussel resources.

With the exception of the mergansers, all diving ducks in the Bay are feeding on benthos found in two fairly distinct habitats, soft and hard bottom areas. Soft bottom areas of typically silty to sandy substrate have a predominance of infaunal organisms such as clams, amphipods, isopods, and polychaetes. The clams found in silty areas are predominantly deposit-feeding clams such as the Baltic Macoma, which feed on organic material from the water column that is deposited on the bottom sediment. Clams found in more sandy areas are filter (or suspension) feeders such as the Soft Shell Clam and Dwarf Surf Clam. Bay ducks and Ruddy Ducks seem to prefer this soft bottom habitat, which is reflected in their food choices. Ruddy Duck increases in recent years in the Bay may reflect their ability to winter in areas near cities such as Baltimore, MD, and Washington, D.C., where they find adequate benthic animal food (Stark 1976) and are relatively safe from hunting.

Most of the seaducks, however, are more closely associated with hard bottom areas where moving tidal water seems to provide conditions suitable for oyster bars and the sessile Hooked Mussels attached to them. Recent boat surveys of Surf Scoter distribution in mesohaline areas of the Bay show a close relationship with this type of habitat (DMK, unpublished data). The relationship between the Eastern Oyster and Hooked Mussel may be an important factor in seaduck management. Oyster bar restoration could be a major asset to restoration of seaduck habitats, as there are few areas in the Bay where rocks and other hard substrates occur that can be used for attachment by oyster spat and mussel larvae. The filter-feeding clams, such as the Dwarf Surfclam and Gemclam, are distributed widely in the Bay, but occur mostly in sandy areas intermediate between the soft muddy sediments and the hard oyster bars.

The overall low percentage of vegetation taken as food by the diving ducks indicates that the ducks rely on a high protein animal diet, which is metabolized as energy during the winter. Perry *et al.* (1986) found that Canvasbacks on a low energy-high protein diet ate more food than Canvasbacks on a high energy-low protein diet. However, in spite of *ad libitum* food, ducks on low energy diets did not obtain the same energy values, indicating that ducks may be unable to adjust intake rates to compensate for low energy foods or that they eat up to a threshold, which is still not equivalent to high energy values.

Factors other than diet of course also may affect the Bay's waterfowl populations. Seaduck populations also have been more affected by disease than other Bay species with three major outbreaks (1970, 1978, 1994) of avian cholera in Chesapeake Bay (Hindman *et al.* 1997). In recent years diving ducks wintering in the Bay have been sampled for avian influenza, but to date there have been no positive findings (C. Driscoll, MD DNR, pers. comm.). Contaminants are ubiquitous along the East Coast of the U.S., however in the Chesapeake, the major problem areas seem to be restricted to the urban harbor areas of Baltimore, Washington, and Norfolk (Perry 1987; Rattner and McGowan 2007). Ruddy ducks and other species of diving ducks that feed in waters near metropolitan areas may be dependent upon tubifex worms (Stark 1976) and other pollution-tolerant species, which possibly makes them vulnerable to higher mortality due to contaminants (Miles and Tome 1997).

MANAGEMENT CONSIDERATIONS

When considering the future of diving ducks in Chesapeake Bay, it is important that managers, hunters, and all Bay enthusiasts are aware of the role of waterfowl in the ecological, economic, and recreational fabric of the Bay. Current and future numbers should be judged on what potential populations can be sustained in the Bay, without causing negative effects to their own habitat or the interests of humans. The Bay might support many more ducks than at present, if restoration programs for oysters and submerged aquatic vegetation are successful.

Declines in scoter and Long-tailed Duck in the Chesapeake Bay in the 1980-90s should be of concern to waterfowl managers as they may reflect increased vulnerability to hunters. There appears to be increased guide service for seaduck hunting in the Bay in recent years, and these hunts are located on major feeding areas. Increased guided seaduck hunting might be related to decreased guided hunts for Canada Goose (*Branta canadensis*) hunting following restrictive regulations on geese. Differential vulnerability to hunting could be a reason for noted changes in the distribution and species composition among the scoters in the Bay as it was noted previously in New England (Stott and Olson 1972). Although there have been major changes with some species during some periods, the long-term trends of seaducks show that numbers in recent years (1990-2006) have not increased as dramatically as other diving ducks (bay ducks and Ruddy Ducks) since the 1950s.

Chesapeake Bay critically needs sanctuary areas where diving ducks are not disturbed by hunters, commercial watermen, or recreational boaters, and where waterfowl can rest and feed (Erwin *et al.* 1993). Without these areas, waterfowl will be forced to expend energy on moving to alternate habitats due to the extensive human uses of the Bay, and their condition for winter survival and breeding will be degraded. Open water sanctuaries may be especially beneficial to diving ducks (Haramis 1991a) and geese. These open water sanctuaries also should be integrated with larger ecosystem protection and restoration measures (i.e., oyster bars) in order to provide adequate habitat and ecosystem function. Freshwater impoundments near the Bay in upland sites could be of benefit to some species of diving ducks and should be constructed in greater numbers where appropriate circumstances exist. The Chesapeake Bay Waterfowl Policy and Management Plan (Chesapeake Executive Council 1990) mentions several of the above suggestions, but little progress has been made in implementation due to lack of funding.

Although actions (e.g., sanctuaries and impoundments) directed towards diving ducks in Chesapeake Bay may not affect continental populations, it might make major differences in the Bay and serve as an example to the rest of the country. Managers must be more proactive to initiate these changes, as it is obvious that past actions have not obtained the desired results. Wildlife managers should fully evaluate the role of private hunting areas, which now are providing thousands of hectares of land for wildlife and probably reducing the pressure on public areas of the Bay. Diving duck population goals should be set higher and management decision enforced.

Diving duck populations may be maintained at current levels through manipulation of hunting regulations, but major increases of ducks, especially seaducks, should not be expected until improvements occur in the quality of habitat in Chesapeake Bay and elsewhere. Major changes in the management of diving ducks may be necessary due to increasing human populations in the Chesapeake Bay area, which is resulting in the degradation of foraging habitat and greater use of open water areas by recreational boating. Managers also need to continue to improve surveys of diving ducks, especially seaducks, so that populations of ducks can be better understood in connection with habitat changes.

ACKNOWLEDGMENTS

We thank the numerous persons that have conducted aerial surveys during the last 52 years and also the many persons that have conducted the food habits analyses that form one of the best long-term databases in biology. We particularly thank the persons who assisted in the data analyses and editing for this manuscript, especially Marie Brady, Marcia Holmes, and Whitney Walker-Mehrhof. We thank several anonymous reviewers and also Caroline Bond, Michael Erwin, Douglas Forsell, Michael Haramis, Roberto Llanso, Scott Petrie, Barnett Rattner, and Christopher Swarth, who offered valuable technical editorial comments.

LITERATURE CITED

Arber, E., Ed. 1910. Travels and Works of Captain John Smith, President of Virginia and Admiral of New England 1580-1631. Part 1. John Grant, Edinburgh, United Kingdom.

Audubon, J. J. 1840. The Birds of America. John James Audubon and J.B. Chevalier, New York.

Austin, J. E., A. D. Afton, M. G. Anderson, R. G. Clark, C. M. Custer, J. S. Lawrence, J. B. Pollard and J. K. Ringelman. 2000. Declining scaup populations: issues, hypotheses, and research needs. Wildlife Society Bulletin 28: 254-263.

Caithamer, D. F., M. Otto, P. I. Padding, J. R. Sauer and G. H. Haas. 2000. Sea ducks in the Atlantic flyway: population status and a review of special hunting seasons. U.S. Fish and Wildlife Service, Laurel, Maryland.

Chesapeake Executive Council. 1990. Chesapeake Bay waterfowl policy and management plan. Chesapeake Bay Program, Environmental Protection Agency, Annapolis, Maryland.

Cottam, C. 1939. Food habits of North American diving ducks. USDA, Bureau of Biological Survey, Technical Bulletin No. 643, Washington, D.C.

Eggeman, D. R. and F. A. Johnston. 1989. Variation in effort and methodology for the midwinter waterfowl inventory in the Atlantic Flyway. Wildlife Society Bulletin 17: 227-233.

Elliot, R., Ed. 1997. Conservation issues for North American sea ducks—a concept paper for a sea duck joint venture under the North American Waterfowl Management Plan. Canadian Wildlife Service, Ottawa, Ontario, Canada, and U.S. Fish and Wildlife Service, Washington, D.C.

Elman, R. 1980. The Atlantic Flyway. Winchester Press, Baltimore, Maryland.

Erwin, R. M., G. M. Haramis, D. G. Krementz and S. L. Funderburk. 1993. Resource protection for waterbirds in Chesapeake Bay. Environmental Management 17: 613-619.

Forbush, E. H. 1912. A history of the game birds, wildfowl and shore birds of Massachusetts and adjacent states. Massachusetts State Board of Agriculture, Commonwealth of Massachusetts, Boston.

Forbush, E. H. 1913. Useful birds and their protection. Massachusetts State Board of Agriculture, Commonwealth of Massachusetts, Boston.

Goudie, R. L., S. Brault, B. Conant, A.V. Kondratyev, M. R. Petersen and K. Vermeer. 1996. The status of sea ducks in the North Pacific rim: toward their conservation and management. Transactions of the North American Wildlife and Natural Resources Conference 59: 27-49.

Grinnell, G. B. 1901. American duck shooting. Forest and Stream Publishing Co., New York.

Haramis, G. M. 1991a. Canvasback *Aythya valisineria*. Pages 17.1-17.10 *in* Habitat Requirements for Chesapeake Bay Living Resources, 2nd ed. revised (S. Funderburk, S. Jordan, J. Mihursky and D. Riley, Eds.). Chesapeake Research Consortium, Solomons, Maryland.

Haramis, G. M. 1991b. Redhead *Aythya americana*. Pages 18.1-18.10 *in* Habitat Requirements for Chesapeake Bay Living Resources, 2nd ed. revised (S. Funderburk, S. Jordan, J. Mihursky and D. Riley, Eds.). Chesapeake Research Consortium, Solomons, Maryland.

Haramis, G. M., J. D. Nichols, K. H. Pollock and J. E. Hines. 1986. The relationship between body mass and survival of wintering canvasbacks. Auk 103: 506-514.

Hindman, L. J., W. F. Harvey, IV, G. R. Costanzo, K. A. Converse and G. Stern, Jr. 1997. Avian cholera in ospreys: first occurrence and possible mode of transmission. Journal of Field Ornithology 68: 503-508.

Horton, T. and W. Eichbaum. 1991. Turning the Tide: Saving the Chesapeake Bay. Island Press, Washington, D.C.

Huesmann, H. W. 1999. Let's get rid of the Midwinter Waterfowl Inventory in the Atlantic Flyway. Wildlife Society Bulletin 27: 559-565.

Jorde, D. G., G. M. Haramis, C. M. Bunck, J. E. Hines and M. A. Mack. 1992. A survey of Macoma clams in the middle and upper Chesapeake Bay. U. S. Fish and Wildlife Special Report, Patuxent Wildlife Research Center, Laurel, Maryland.

Kehoe, P. 1994. Status of sea ducks in the Atlantic Flyway. Report of the *Ad Hoc* Sea Duck Committee, New Brunswick Department of Natural Resources and Energy, Fredericton, New Brunswick, Canada.

Lovvorn, J. R. 1989. Distributional responses of canvasback ducks to weather and habitat change. Journal of Applied Ecology 26: 113-130.

Matthiessen, P. 1959. Wildlife in America. Viking Press, New York.

Martin, A. C., R. H. Gensch and C. P. Brown. 1946. Alternative methods in upland gamebird food analysis. Journal of Wildlife Management 10: 8-12.

Miles, A. K. and M. W. Tome. 1997. Spatial and temporal heterogeneity in metallic elements in industrialized aquatic bird habitats. Environmental Pollution 95: 75-84.

Munro, R. E. and M. C. Perry. 1981. Distribution and abundance of waterfowl and submerged aquatic vegetation in Chesapeake Bay. Final report to Fish and Wildlife Service/Office of Biological Survey 78/D-X0391. Chesapeake Bay Program, U.S. EPA, Annapolis, Maryland 180.

Newell, R. 1988. Ecological changes in Chesapeake Bay: are they the result of over-harvesting the American oyster, *Crassostrea virginica*? Pages 536-546 *in* Understanding the Estuary: Advances in Chesapeake Bay Research (M. Lynch and E. Krome, Eds.). Chesapeake Research Consortium, Baltimore, Maryland.

Nichols, J. D., J. E. Hines, J. R. Sauer, F. W. Fallon, J. E. Fallon and P. J. Heglund. 2000. A double-observer approach for estimating detection probability and abundance from point counts. Auk 117: 393-408.

Orth R. J. and K. Moore. 1983. Chesapeake Bay: an unprecedented decline in submerged aquatic vegetation. Science 223: 51-52.

Orth, R. J., T. J. B. Carruthers, W. C. Dennison, C. M. Duarte, J. W. Fourqurean, K. L. Heck, Jr., A. R. Hughes, G. A. Kendrick, W. J. Kenworthy, S. Olyarnik, F. T. Short, M. Waycott and S. L. Williams. 2006. A global crisis for seagrass ecosystems. BioScience 56: 987-996.

Perry, M. C. 1987. Waterfowl of Chesapeake Bay. Pages 94-115 *in* Contaminant Problems and Management of Living Chesapeake Bay Resources (S. K. Majumdar, L. W. Hall, Jr. and H. M. Austin, Eds.). The Pennsylvania Academy of Science, Philadelphia.

Perry, M. C. and F. M. Uhler. 1981. Asiatic clam (*Corbicula manilensis*) and other foods used by waterfowl in the James River, Virginia. Estuaries 4: 229-233.

Perry, M. C. and F. M. Uhler. 1988. Food habits and distribution of wintering canvasbacks (*Aythya valisineria*) on Chesapeake Bay. Estuaries 11: 57-67.

Perry, M. C. and A. S. Deller. 1995. Waterfowl population trends in the Chesapeake Bay area. Pages 490-504 *in* Proceedings of the 1994 Chesapeake Research Conference. Toward a Sustainable Watershed: The Chesapeake Experiment (P. Hill and S. Nelson, Eds.). CRC Publication No. 149. Chesapeake Research Consortium, Edgewater, Maryland.

Perry, M. C. and A. S. Deller. 1996. Review of factors affecting the distribution and abundance of waterfowl in shallow-water habitats of Chesapeake Bay. Estuaries 19: 272-278.

Perry, M. C., R. E. Munro and G. M. Haramis. 1981. Twenty-five year trends in diving duck populations in Chesapeake Bay. Transactions North American Wildlife and Natural Resources Conference 46: 299-310.

Perry, M. C., W. J. Kuenzel, B. K. Williams and J. A. Serafin. 1986. Influence of nutrients on feed intake and condition of captive canvasbacks in winter. Journal of Wildlife Management 50: 427-434.

Petersen, M. R. and M. E. Hogan. 1996. Seaducks: a time for action. International Waterfowl Symposium 7: 62-67.

Rattner, B. A. and P. C. McGowan. 2007. Potential hazards of environmental contaminants to avifauna residing in the Chesapeake Bay estuary. Waterbirds 30 (Special Publication 1): 63-81.

Reed, N. P. and D. Drabelle. 1984. The United States Fish and Wildlife Service. Westview Press, Boulder, Colorado.

Salyer, J. C. 1934. A program of waterfowl restoration. Circular No. 339. U.S. Department Agriculture, Washington, D.C.

Serie, J. and R. Raftovich. 2006. Atlantic flyway waterfowl harvest and population survey data. U.S. Fish and Wildlife Service, Office of Migratory Bird Management, Laurel, Maryland.

Stark, R. 1976. Feeding ecology of the ruddy duck in Pennsylvania. M.S. Thesis, Pennsylvania State University, University Park, Pennsylvania.

Stewart, R. E. 1962. Waterfowl populations in the Upper Chesapeake Region. Special Scientific Report Wildlife No. 65. U.S. Fish and Wildlife Service, Washington, D.C.

Stott, R. S. and D. P. Olson. 1972. Differential vulnerability patterns among three species of sea ducks. Journal Wildlife Management 36: 775-783.

Stott, R. S. and D. P. Olson. 1973. Food-habitat relationships of seaducks on the New Hampshire coastline. Ecology 54: 996-1007.

Swanson, G. A. and J. C. Bartonek. 1970. Bias associated with food analysis in gizzards of blue-winged teal. Journal of Wildlife Management. 34: 739-746.

Swanson, G. A., G. L. Krapu, J. C. Bartonek, J. R. Serie and D. H. Johnson. 1974. Advantages in mathematically weighting waterfowl food habits data. Journal of Wildlife Management. 38: 302-307.

Udall, S. L. 1963. The Quiet Crisis. Avon Books, New York.

Walsh, H. M. 1971. The Outlaw Gunner. Tidewater Publishers, Cambridge, Maryland.